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THE AMERICAN SOCIETY OF NATURALISTS
CHANCE OR PURPOSE IN THE ORIGIN AND EVOLUTION OF ADAPTATION[1]

THE naturalist lives surrounded by fellow men, whose ideas concerning the origin of living things are still totally at variance with his own. To them creation is a historical drama, and with the act of creation its *purpose* was fulfilled. The naturalist lives surrounded by fellow animals, that show on the whole no change except the chance fluctuations of the seasons or of the years. They give to ordinary observation every evidence of permanency, but no evidence of evolution, and only the highly specialized student reports at times the appearance of new forms.

It is surprising, with these deadening influences always present, that we should sometimes fail to fully realize that evolution is a process now taking place in the same way that it has taken place in the past; that it is a process that we can study directly; something that possibly we can control and direct, and upon our knowledge of which the destiny of the human race may depend.

Convinced that evolution has taken place, admitting that it is still going on, nevertheless the position of the naturalist in regard to the causes of evolution is far from satisfactory and most unsatisfactory concerning the *origin and evolution of adaptation.*

The evidence that evolution has taken place we owe primarily to the paleontologist, but it is historical evidence, at best,

[1] Presidential address at the dinner of the American Society of Naturalists in Boston, December 29, 1909.

and history, as Voltaire said, is "a permanent pleasantry whose sense escapes us."

It is the sense of the process that escapes us. Comparative anatomy has built up a monument of industry, but the foundations lie in the sand. The *assumption* of the theory of evolution makes intelligible the whole of comparative anatomy as no other theory has ever done, and has led many biologists to conclude that it is, therefore, a correct interpretation. I, for one, do not doubt this, but comparative anatomy has nothing serious to say concerning the factors of evolution.

And if we turn to my favorite field of embryology, what is the answer? Von Baer, who enunciated one of the fundamental generalizations of embryology, did not accept the theory of evolution. The recapitulation theory, the most widely accepted statement in regard to the historical side of embryology, has been exaggerated, overdone, and in some quarters thrown into the waste heap of premature speculation. I do not doubt that it aroused a young generation to great enthusiasm for investigation, nor do I doubt that the study of embryology furnishes many clues to the relationships of animals; but I venture to affirm that it has done nothing to advance our knowledge of the *causes* of evolution.

Are we not in rather a hazardous position concerning our belief in the evolution of adaptation? It may be a belief more in accordance with known facts than its great rival, the theory of special creation, but however convinced of its truth, we remain unsatisfied until we can tell how evolution and adaptation have taken place, how they are going on at the present time, and what the future has in store for us.

I hear some one say, "But we know how evolution has taken place; by natural selection." "Perhaps," says his neighbor, "but the Lamarckian principle is the chief agent of adaptation." "Maybe," says a third, "but the environment has had more to do with the origin of species than any other factor, and 'we can prove it.'" "No," says the psychologist, "it is the will to live that brings about evolution, for it is the creative principle of evolution—l'élan de la vie." And the pragmatic philosopher, at the head of the table, adds, "You are all right, my children, evolution has taken place in whatever way you find it advantageous to think of the process."

Comment seems superfluous, but in the flux of opinion concerning the process of evolution there are two general points of view of fundamental moment for every thinking man.

To the majority of evolutionists accepting the theory of natural selection, evolution is the result of accidental variation; it is haphazard or due to chance. By taking this ground the selectionist feels that he stands on the evidence of facts, for "chance" variations he holds can be demonstrated to occur, and secondly that he escapes the onus of explaining how the adaptive variations arise, for he believes that there is no relation between the creation of something new and the part it subsequently plays in the welfare of the species.

But to other minds, or temperaments, such a conception of the origin of the living world seems inconceivably crude. To them it seems beyond comprehension that the evolution of a man, for instance, from an amœba, for example, has been due only to accidental or chance happenings. They *feel* that some more direct and intimate relation must exist between the origin of a new part and the use it comes to subserve.

Grant that many false steps have been made, admit that countless individuals

have been born to perish, what has given us the *progressive* chains of beings? Chance, says one extreme view; purposeful response, says the other.

I need not repeat before this body of naturalists that to-day we have dropped entirely the antiquated use of the word chance as something not subject to the laws of mechanics. That conception of chance arose, no doubt, because chance events are those that can not be predicted individually and what he can not predict seems to the confused thinker to disobey the causal law. Out of his ignorance he imagines blind happenings.

We mean by chance, in ordinary speech, two main things. "I chanced to be there," we say, meaning that our being there was not connected with what occurred, not that mysterious forces, instead of two legs, carried us there. The other meaning is that of a large number of possible combinations a particular one happened.

Darwin used chance *variations* as synonymous with fluctuating variations. He clearly understood that a chance variation is one due to some unknown cause or combination of causes.

But it is the other sense of the word chance that is of capital import for the matter we have in hand. In this sense chance means that a variation having appeared, *chanced* to find a suitable environment. In this latter sense only is it desirable to use the word chance in connection with organic evolution. The confusion of this meaning with the other one which applies to the *origin* of a variation has led to a regrettable obscurity in the minds of some evolutionists.

Darwin's famous book is entitled "The Origin of *Species*" but his theory of natural selection explains the *adaptations* of living things. Darwin was in a large measure concerned with demonstrating that species, in the Linnæan sense of species, arose by evolution, not by special creation. He has himself said:

> Hence if I have erred in giving to natural selection great power, which I am very far from admitting or in having exaggerated its power, which is in itself probable, I have at least, as I hope, done good service in aiding to overthrow the dogma of separate creations.

But to-day, accepting evolution, we are concerned as to whether the theory of natural selection explains the *origin of species*, or whether it explains the *adaptations* of animals and plants. These two questions have often been merged into one, yet it is notorious that, by systematists, specific distinctions rest in many cases on differences that have no adaptive significance whatever.

If, then, the systematist's definition of species is what we mean when we speak of species, and this definition does not concern adaptive characters (or only incidentally) clearly it is futile to attempt to explain the *origin of species* by the theory of natural selection.

Curiously enough, we do, I think, when speaking of *adaptation*, attach one meaning to the word species and another meaning when speaking of *evolution*. In the latter case we often fall back upon the definitions of the systematist. When we speak of the evolution of adaptations, through natural selection, however, we are thinking of organisms as groups that are structurally and functionally adapted in different ways to the environment in which they live, and differ from all other groups in these relations to the environment. These adaptive characters do not, however, in most cases lend themselves to sharp definition for purposes of identification and are shunned, therefore, by the systematist. If I am right on this point, the characters of systematic zoology are, at most, only parts of adaptive structures

and are generally only by-products of the process of evolution—characters that belong for the most part to the dump-heap of evolutionary advance; and whilst they, like all characters, call for explanation, the student of adaptation of the living world (regarding adaptation as the fundamental problem of evolution) will pass them over as of trivial importance for his ends.[2]

Our problem, then, concerns the adaptations of species, and from this time forward when I speak of the origin of species I mean the origin of the adaptive characters of species.

Modern thought has rejected the theological view of the miraculous origin of animals and plants, but philosophy still discusses the question whether there is something purposeful residing in matter or controlling matter that has brought about the adjustments between the animal and its environment, while science turns rather to the question whether adaptation is not the result of a reaction between the organism and the outer world; and if so, in what sense we are justified in applying chance to such a process. Let us examine briefly the philosophical and scientific points of view.

We have sufficient evidence to show that animals and plants *sometimes* respond directly in an adaptive way to changes in their environment; to such agents as food, or light, heat and cold, moisture and dryness.

When we recall that since the first beginning of life on the earth, plants and animals have been subjected to these kinds of physical influences, and the forms that have persisted are those that have reacted adaptively, it is not surprising that they should respond at times, if not always, adaptively even under new conditions. The fact that some directly adaptive responses occasionally occur can not, however, be used as an argument that all adaptive responses have so arisen.

The adaptive response to poisons, or to foreign bodies of any kind introduced into the animal, is one of the most remarkable phenomena of adaptation. In the great majority of cases the response is specific for a particular poison, and the poison, such as abrin, may be one with which the animal can have had no previous experience. A leading pathologist has not hesitated to state in this connection:

> If our studies in infection and immunity have any meaning, they teach us, that . . . adaptation is primarily an active process or at least inevitable and in no sense subject to chance. It is not the mere fortuitous, passive modification of living matter in a favorable direction, but a process whereby that living matter is able to a greater or less extent to change and suit itself to its environment.

The adaptive character of these responses loses some of its mystery, although none of its interest, if, as has been suggested, the poison acts by becoming first incorporated in the living tissue and the living tissue in consequence sets free certain products of the reaction or possibly products of its own break-down whose presence in the blood serves to lock up the poisonous substances. It has been suggested that this process is similar in many ways to the process of assimilation of food by the organism. If this point of view recommends itself, it shows how the organism is a machine already prepared to do this sort of work, and the cases that fill us with astonishment may turn out to be but variations of a process essential to all metabolism.

[2] This statement is not, of course, to be understood to underrate the great value of systematic work; I wish only to emphasize that the evolution of adaptive characters, rather than of systematic characters, is the question of absorbing interest to the naturalist.

More familiar is that class of adjustments by means of which, through use of a part, its functional activity becomes more effective; the muscle grows strong, the skin thickens, the iris contracts and even the bones bear witness to stresses and strains. Here also we are beginning to see that these adjustments may be nothing more than extensions of the normal processes of growth—function breeds function, because the very act of functioning is itself a step towards further change in the same direction.

One of the most remarkable adaptations is the development of a whole embryo out of half of an egg. But here, too, we have come to see that the result is not due to any special and sudden development of a new and wonderful power, but that the regulative process is a simple expression of the same processes that are at work in normal development. The marvel is no more, no less, than that of development itself.

These four great groups include many of the most important kinds of adaptive responses shown by organisms. We can not afford, I think, to underestimate their importance. But observe! They all concern the individual; they tell us nothing in regard to the next generation. Yet even here there has been slowly accumulating in recent years evidence to show that *some* of the external agents that affect the soma or body of the individual may affect the eggs in the ovary of that individual in exactly the same way.

This evidence fails, however, to show that it is the adaptive responses only that take place alike in germ and soma. The evidence indicates at most that certain kinds of external factors may affect soma and germ in the same way, and that these effects apply equally to beneficial, indifferent and baleful results. There is no satisfactory evidence in favor of the view that specific structures produced first in the soma can be transmitted from soma to germ; and least of all is there any evidence that the eggs or the sperms are affected by the psychic experiences of the body. Yet it is this latter idea to which the Lamarckian school has so often appealed. In recent times the Lamarckian has played a losing game. He has been driven from pillar to post and failed to make good many of his claims, which, if true, should furnish the fairest opportunity for demonstration that the whole field of adaptation has to offer.

We find in this connection a significant fact. Nature has not hesitated to insert an unspecialized egg and sperm between every link in the evolutionary series. She seems more concerned in transmitting a material sensitive to external responses than the effects of previous responses themselves.

We are now in a position to attack what is generally conceded to be the central problem of adaptation. It is held that the crucial test of any theory of adaptation is found in those cases where special contrivances exist, that could not have arisen through action and reaction in a causal sense: for example, in many insects the male and female organs of copulation show close adjustments to each other; those of the male having parts that fit precisely corresponding parts of the female. These fittings vary from species to species, and a change in the male finds a corresponding change in the female of the same species. I shall call these lock and key adaptations—structures and functions complete at birth of the organism. It is a consideration of these adaptations that has separated the naturalists as a class from the physiologists, and has drawn the nat-

uralists and philosophers together—for better, for worse.

Many other illustrations will occur to every naturalist: for instance, the instinct of the caterpillar to spin a coccoon that serves as a protection not so much for itself as for the future pupa, the instinct of the spider to make a web to catch a prospective fly, or of a bird to build its nest for eggs not yet in sight; the occurrence of offensive odors or poisons, or of organs that act as a passive defense for the animal as the spines of the hedgehog or of the sea-urchin, or the colors of animals that may at times serve to protect them. Zoologists have, I think, often let their imagination run riot concerning some of these adaptations, but there remains enough that is probable to satisfy the most sceptical.

I have said that we can not afford to underestimate the *directly adaptive* responses shown by the body, and I have intimated that these are only elaborations of already existing functions. Let me add that the naturalist has equally felt that he can not afford to neglect the lock and key adaptations. The alliance between philosophy and biology is due to the fact that these contrivances are not the result of primary, or directly causal relations, but are secondary relations, which appear to be removed from the province of physical problems in the sense that they are supposed *not* to be the result of causal interaction. It is in this aspect of the subject that chance and purpose bloom forth in all of their significance and danger. It is here, therefore, that it is our duty as scientists to make careful inquiry into what causes the lock to vary and what the key and to discover, if possible, whether there exists any mechanism to insure that they shall continue to vary along the same lines.

Perhaps the following somewhat shopworn case may further illustrate my meaning.

The long coiled proboscis of sphinx moths permits them to reach the juices at the bottom of flowers with a tubular corolla. The proboscis is fully formed when the moth emerges from the pupa and its use has no influence in increasing its length. The proboscis is to the corolla what the key is to the lock and yet the lock can have no causal, *i. e.*, direct influence in shaping the key.

If we exclude the Lamarckian explanation, we find many relations of this sort. The speed of the hare bears no causal relation to that of the fox. We can not think of the fox in the sense of a physical environment acting on the germ cells of hares; yet without the fox the hare would, we feel confident, never have developed the long hind legs. In brief, the zoologist has come to look upon contrivances of this kind as the very essence of adaptation. He finds himself in consequence facing two alternatives, neither of which is he anxious to accept. On the one side are the champions of chance; on the other, the apostles of purpose. The issue may *seem* to have reduced itself to these alternatives.

I beg your attention for a little while to consider the import of this decision, and I will take Bergson's view in his "L'Évolution Créatrice" as the clearest and most profound expression of the hypothesis that adaptation of the living world is the outcome of a creative force that shapes matter for an immediate purpose, though not according to a preconceived or predetermined purpose. Many philosophers have assumed a creative principle of some kind that directs the organic world, but have generally taken an anthropomorphic conception of the process. Bergson, on the other hand, conceives of creation without

a creator—he formulates a creative principle that does not postulate the doctrine of finality. His élan vital adjusts itself to each new need that arises; does not work on a preconceived or foreordained plan, but adapts itself to the matter and to the situation in the same way in which an inventor will take the materials at hand and shape them to his purpose with the tools at his command.

It seems to me—I may be wrong—that this theory of the origin of adaptation will not find wide acceptance with the militant evolutionist of to-day; and I shall attempt to formulate the reasons why it seems to me he is likely to refuse to accept so attractive a view, even when so persuasively presented.

In the first place, the theory tells us everything and tells us nothing. It solves the problem by begging the question. An internal principle of which we know nothing steps in like the fairy in the story and does all that is required.

In the second place, Bergson's theory attempts to solve one of the ultimate problems of biology by *a priori* argument—a method from which science has suffered much and has come to look upon askance. Our experience in studying living things teaches us that only by patient labor extending over many years are we likely to gain a little insight into even the simplest modes of action. We feel that there is no royal road to the solution of such complex questions.

And lastly, Bergson's theory, like many of its kind, directs its attention to that side of the problem that is entirely beyond our present ken, namely, the intimate nature of the reaction itself. It lays in consequence on the problem an emphasis that is foreign to our scientific discipline. It may be good philosophy or excellent metaphysics, but it distracts the scientist from his more modest aspirations. It is as though the physicist directed his attention to an explanation of why hydrogen combining with oxygen should give the qualities that we recognize in water; or why the particle of sodium chloride should give a crystal having the form of a cube. If the chemist or physicist disclaims any such ambition, how much more must the biologist disclaim any knowledge—nay, the possibility of any such knowledge, at present, of the behavior of highly complicated organic matter.

If from the point of view of the working evolutionist I have ventured to criticize Bergson's "L'Évolution Créatrice," I beg that you will not understand me to say that I am unappreciative of its value in other directions. On the contrary, as a contribution to speculative metaphysics, it has unusual fascination; as a contribution to that higher form of literary art that we call philosophy, it is an admitted masterpiece. But the day is fast disappearing when the scientific study of evolution can be exploited for literary purposes—except for literary purposes. Paper evolution has fallen into disrepute.

If then we fail to find intellectual satisfaction in the idea that adaptations have arisen as a conscious response of the animal, what alternative does the *theory of chance* offer?

The only legitimate sense in which chance can be applied is, as I have said, that the variations happened, *i. e.*, chanced, to find an environment suited to them. In this sense we speak of evolution as a chance result. Nevertheless, I think most of us feel, as I have said, that there must be some closer bond than chance that insures the *continuance* in a given direction of variations once begun. Even Weismann, a typical neo-Darwinian, admitted in his interesting essay on Germinal Selec-

tion, that unless we can find such a relation, the whole fabric of natural selection falls to the ground; and, as is well known, he attempted to supply this deficiency in his competition of the biophors in the germ-cells. His attempt has failed, on the whole, to bring conviction that the result has been reached in this way, but his statement, in regard to the weakness of the appeal to chance, has, I believe, struck a responsive cord.

It seems to me that we get a suggestion of how continuous adjustment is more likely to occur if we refer variations not to internal conflicts of the biophors, but to the action of external factors on the germ plasm, and *assume* that germinal material that shows itself susceptible of change in an environment is more likely to show further variations in the same direction in that environment.

On some such view we can better understand how evolution along adaptive lines is more likely to give further variations in the same direction, and there is not a little evidence in favor of this view in the history of domesticated animals and plants. After the first step, which was undirected, *i. e.*, not purposeful, the subsequent events are rendered more probable; for the dice are loaded. Evolution along adaptive lines would be a consequence of the very processes that variation has initiated.

The same idea shows how incipient stages of organs may progress until they become of positive advantage to the race and may ultimately carry it along a progressive line of evolution; or should the variation be baleful, lead in its ultimate development to the destruction of the species.

Turning now to another aspect of the subject, I think that our ideas concerning chance and purpose have been largely influenced by those creative processes in which man himself *seems* to have played a leading rôle. I refer to the artificial production of our domesticated animals and cultivated plants.

We owe to Darwin chiefly a comparison between certain features in the development of adaptation under domestication and the development of adaptation in nature.

Domesticated hens lay more eggs than *Gallus bakkiva*. Cows give more milk than buffaloes. Apples in an orchard are larger than in the forest. Potatoes are bigger in a garden than in the wilds of Chili. Why? In part, no doubt, because better conditions of soil or of feeding keep up the product to its maximum, but no one will claim for a moment that the only difference is in the better conditions of food. We realize that the results have not and could not have been obtained from the wild forms at once, but only through a long process of artificial selection by which the domesticated animals have become *adapted* to man's needs.

Admitting this, as one must, what is its bearing on our problem? It is admitted that artificial selection has created nothing new, it has supplied only an opportunity for what already appeared, as new, to remain in existence, but, by picking out the new variation and isolating it under conditions where it can live, *purpose* enters in as a factor, for selection had an end in view.

By preserving the variation the possibility of further variation in the same direction is insured.

We see clearly enough the rôle that chance and purpose play in these processes. The first variation is the result of the environment acting on the organism; it happened, "chanced," to appear at a time when a man was there to give it an opportunity to live. And about its pur-

pose? It could only be said to have purposely *arisen* because it was conscious of a man in its vicinity that would protect it, which is sheer nonsense to most of us. This would mean from Bergson's point of view that cows began to give more milk under domestication because the "élan vital" of the cow made a sacrificial offering to man on the altar of their common interests; that hens laid more eggs on the same altar and that the fancy races of fat pigs have arisen from disinterested or unsophisticated motives so far as the creative principle in the pig is concerned.

But after a new variation had arisen we may speak of purpose as a directive agent in the formation of domesticated races, in the sense that man supplied the purpose when he selected the new variation. The next step was again due to a further action of the environment, but the direction of that action was to some extent prejudiced by what had already taken place. Usefulness to man was the direction in which new variations were made more probable.

Let us see how by adjusting this scheme to nature our alternative of chance or purpose fares. As before, we assume a first variation arises through external factors. If it finds a suitable place it survives. Here there is no purpose unless in the far-fetched sense that finding the external world suited to itself "is a purpose"; rather is the result due to chance. But there is another side to the question from the Darwinian point of view; for, while it is admitted that chance may in some cases have to do with survival as just defined, yet survival is due on the whole more often to *competition;* when the race is to the swift and the battle to the strong. It is for a purpose that an organism crowds out its competitors, for the purpose of survival—not conscious purpose, perhaps, but in a different sense the *result* is purposeful. So I think by a shifting of the angle of vision one might come to look upon survival in nature as purposeful in the same sense in which that term is applied to artificial selection. By this substitution the old and familiar phrase, purpose, might still be applied in a *perverted sense* to the theory of natural selection, and possibly the popular extension of the theory may have been in part due to the easy psychological transition thus afforded.

But does this conception of the evolution of adaptation accord with our experience? Is the battle always to the brave—for the brave is sometimes stupid—or the race to the swift, rather than to the more cunning? Have we here a true picture of the evolution of adaptation?

An individual advantage in one particular need not count much in survival when the life of the individual depends on so many things—advantages in one direction may be accompanied by failures in others, chance cancels chance. Take, for example, the human race, the conditions of which we know perhaps better than those of any other. An individual may be highly gifted in one direction compared with his fellows. He may win a Marathon, or have more intelligence; he may have a better physique, or a more perfect digestion; but he does not therefore necessarily leave more descendants even if his advantages bring material and social rewards. There are no records, so far as I know, to show that we can trace back to only a single pair of superior individuals any preponderating number of individuals of succeeding generations; often the reverse is observed, for the more highly gifted often have fewer offspring. It seems to me that what we know is at variance with the widely accepted interpretation that the individual

through his own advantages replaces by means of his offspring the rest of the population. Rather do we find that the progressive races are those in which the environment causes definite variation in the largest number of advantageous directions. The race advances by the accumulation of these variations. Many individuals of the race contribute towards its maintenance by adding to its advantages, some in one way, some in another. And they do so, not by supplanting their fellows, for each advantage to be gained, but by combining with them. The new variations are the products of the environment. Their perpetuation by grafting on to the race raises the race to a level from which further variations in the same direction are possible. Sexual reproduction comes to have an unexpected meaning, for through it the contributions of the individuals are added to the race. It seems to me that some such interpretation as this is more nearly in accord with our present knowledge of the origin of adaptation. If so, we should expect advance in the human races to take place not by every man's hand being raised against his neighbor, nor by the picking out of a few choice individuals in the way the breeder produces new varieties of corn, horses, pigeons and pigs, but we should expect advance to take place in those parts of the world where there is a good stock to start with, and an environment that calls forth in that stock favorable variations in excess of unfavorable ones.

It seems preposterous to us that so highly organized a machine as the human body could have evolved by undirected variations and chance combinations from a formless mass of living matter. But such a statement of the problem gives a false impression, if, as I have tried to show, each step that the organism has taken guarantees further responses in the same direction. And, since the steps that count are the adaptive ones, the very essence of the process of evolution is such that the organism is carried along adaptive lines. The mechanism of survival (if I may be pardoned the expression) is such that it insures success where it is most called for. To repeat a familiar epigram: In evolution nothing succeeds like success.

In conclusion, I owe you, I fear, an apology for attempting to discuss so serious a theme at this time and occasion, when high living may not be conducive to plain thinking. In the detail of every-day work in which we are plunged we are apt to lose sight of the relative value of the problems at which we work. It seemed to me, therefore, that it might not be inappropriate this evening to focus our attention on the large problem of organic adaptation, which is still, I think, the central problem of the naturalist; and if in attempting an analysis of the present situation I have allowed my imagination too free rein, I submit, in defense, that the human mind has an ineradicable tendency to probe into the unknown, and that the fires of the imagination, kept alive by human curiosity, may also serve a purpose in the progress of human thought, *provided* the imagination is controlled at every advance by an appeal to experience, and is used as a tool and not as an end in itself. But I frankly confess that I feel, as no doubt every one does who tries to keep in touch with modern work, that the time is past when it will be any longer possible to speculate light-heartedly about the possibilities of evolution, for an army of able and acute investigators is carefully weighing by experimental tests the evidence on which all theories of evolution and adaptation must rest. To them belongs the future.

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